FEATURE

Pacific Salmon Prespawn Mortality:

Patterns, Methods, and Study Design Considerations

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Adult Pacific salmon *Oncorhynchus* spp. may reach spawning grounds but perish before reproducing, a phenomenon known as “prespawn mortality” (PSM). This review synthesizes information on PSM rates and estimation methods to evaluate patterns and facilitate study design development. Questionnaire responses from 60 fisheries professionals indicated that female PSM was routinely monitored in numerous Pacific salmon populations, but variations in data collection and reporting could lead to systematic biases in estimates. Reported PSM rates varied among years and locations, ranging from 0% to over 90%. An evaluation of methodological variations within a single data set illustrated that PSM estimates were sensitive to estimation method, the timing and spatial extent of sampling, and inclusion of male data. To improve accuracy of PSM estimates based on carcass data, we recommend frequent surveys during holding and spawning periods, use of spatially and temporally balanced study designs with adequate sample sizes, and separate reporting for males and females.

Mortalidad pre-desove del salmón del Pacífico: patrones, métodos y consideraciones para el diseño de investigación

El salmón adulto del Pacífico *Oncorhynchus* spp. puede llegar a áreas de desove, pero muere antes de reproducirse; fenómeno conocido como mortalidad pre-desove (MPD). En esta revisión se resume la información concerniente a las tasas de MPD y a los métodos de estimación que se utilizan para evaluar patrones que facilitan el desarrollo de diseños de investigación. Las respuestas a un cuestionario aplicado a 60 profesionales de las pesquerías, indican que las hembras con MPD fueron rutinariamente monitoreadas en diversas poblaciones del salmón del Pacífico, sin embargo las variaciones en la colecta y reporte de datos pueden producir sesgos sistemáticos en las estimaciones. Las tasas reportadas de MPD variaron desde 0% hasta 90% entre años y localidades, Una evaluación de las variaciones metodológicas dentro de una misma base de datos, mostró la sensibilidad en las estimaciones de MPD a los métodos utilizados, al alcance espacial y temporal del muestreo y a la inclusión de datos sobre machos. Con el fin de mejorar la precisión de los estimados de MPD basados en muestreo de cadáveres, se recomienda hacer prospecciones rutinarias durante los periodos de desove y retención, valerse de diseños de investigación que equilibren las dimensiones espacial y temporal mediante tamaños de muestra adecuados y reportar de forma separada información de machos y de hembras.

Mortalité avant le frai du saumon du Pacifique : Modèles, méthodes et considérations de la conception de l’étude

Les saumons adultes du Pacifique *Oncorhynchus* spp. peuvent atteindre les frayères, mais périssent avant de se reproduire, un phénomène connu sous le nom de la mortalité avant le frai (PSM). Cette analyse synthétise les informations sur les taux de PSM et les méthodes d’estimation pour évaluer les modèles et faciliter le développement de la conception de l’étude. Les réponses au questionnaire de 60 professionnels de la pêche ont indiqué que les PSM femelles ont été régulièrement contrôlées dans de nombreuses populations de saumon du Pacifique, mais les variations dans la collecte des données et les rapports pourraient conduire à des biais systématiques dans les estimations. Les taux de PSM signalés variaient au fil des années et des lieux allant de 0 % à > 90 %. Une évaluation des variations méthodologiques au sein d’un seul jeu de données a permis d’illustrer que les estimations de PSM étaient sensibles à la méthode d’estimation, au calendrier et à l’étendue spatiale de l’échantillonnage, et à l’inclusion de données du sexe masculin. Pour améliorer la précision des estimations PSM basées sur des données de carcasse, nous recommandons des enquêtes fréquentes au cours des périodes de retenue et de frai, l’utilisation de conception d’études spatialement et temporellement équilibrées avec des tailles d’échantillons adéquats, et des rapports séparés pour les mâles et les femelles.

INTRODUCTION

Adult Pacific salmon *Oncorhynchus* spp. returning to spawning grounds face a number of mortality threats in freshwater prior to reproduction. Premature mortality can occur during upstream migration, termed “en route mortality” (Cooke et al. 2004; Keefer et al. 2008), or after adults reach spawning grounds but prior to successful release of gametes, known as “prespawn mortality” (PSM; Gilhousen et al. 1990; Hinch et al. 2012). High premature mortality rates have been observed in several Pacific salmon species in distinct geographic locations, eliciting concern about the long-term viability of affected populations (Scholz et al. 2011; Hinch et al. 2012). Understanding the role that premature mortality plays in population viability is critical for the management and conservation of many economically and culturally important Pacific salmon stocks (Cooke et al. 2004; Spromberg and Scholz 2011). Additionally, accurate estimates of premature mortality are important for measures of population productivity such as spawning stock size, particularly where spawning escapement is enumerated downstream of spawning areas and may not account for en route and prespawn deaths (Baker and Schindler 2009). Although similar factors can affect both en route and prespawn mortality in some Pacific salmon populations, methods used to estimate mortality during these two stages are typically distinct. In this review, we focus on PSM, also referred to as either egg retention or spawning success (the complement of PSM). Methods for evaluating Pacific salmon en route mortality and investigations into causative factors have been described elsewhere (e.g., Cooke et al. 2006a, 2006b; Keefer et al. 2008).

A variety of proximate causes may contribute to PSM across Pacific salmon populations, and interactions likely occur among factors. Given the physiological demands of long-distance Pacific salmon migrations, some mortality prior to spawning is expected (Quinn 2005), but unusually high PSM rates have been associated with steep declines in some populations, including Fraser River Sockeye Salmon *O. nerka* (Cooke et al. 2004). Elevated PSM in the Fraser River system has been linked to early upstream migration timing, which increases exposure time to pathogens and stressful holding conditions, including high water temperatures (Hinch et al. 2012). Coho Salmon *O. kisutch* populations in the Puget Sound region of Washington have experienced annual PSM rates of 50% to over 90% as a result of exposure to toxins in urban stormwater runoff (Scholz et al. 2011; Spromberg et al. 2015). Life history model projections indicate that such high PSM rates pose a significant extinction risk (Spromberg and Scholz 2011). In Oregon’s

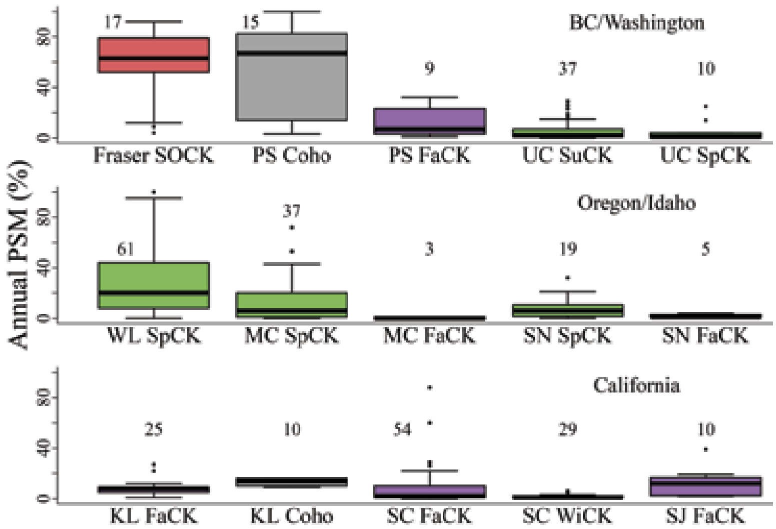

Figure 1. Boxplots show median values (horizontal line), 50th percentile values (box), 90th percentile values (whiskers), and outlier values (open circles) of annual PSM values reported in the literature for Sockeye (SOCK; red boxes), spring Chinook (SpCK; green), summer Chinook (SuCK; green), fall Chinook (FaCK; purple), late-fall/winter Chinook (WiCK; black), and Coho (gray) salmon. Data are from Fraser River, British Columbia (late-run Sockeye Salmon); Puget Sound (PS) and upper Columbia (UC) regions, Washington; Willamette (WL) and mid-Columbia River (MC) basins, Oregon; Snake (SN) River Basin, Idaho; Klamath (KL), Sacramento (SC), and San Joaquin (SJ) river basins, California. Boxes show multiple streams and years combined and sample sizes (combined stream years) are given. Data sources are shown in Appendix 1.

Willamette River Basin, PSM in spring-run Chinook Salmon *O. tshawytscha* has been associated with high water temperatures and poor fish condition (Keefer et al. 2010; Roumasset 2012). Elsewhere, mass spawner die-offs have been linked to anoxia resulting from elevated temperatures and intense crowding in Pink *O. gorbuscha* and Chum *O. keta* salmon (Murphy 1985; Heard 1991). Increased PSM has also been associated with high spawner density (Semenchenko 1988; Quinn et al. 2007) and pathogen outbreaks (Jones et al. 2004; Bradford et al. 2010).

Regardless of study location or species, improved precision of PSM estimates will help researchers identify factors affecting PSM. Consistent and efficient sampling designs will generate more cost-effective and standardized measures of PSM, facilitating comparisons among populations at both local and regional scales. Our study had four objectives: to (1) evaluate broad patterns in PSM across species and regions, (2) review commonly used PSM estimation methods based on a questionnaire completed by fisheries professionals throughout the North American range of Pacific salmon, (3) use a detailed data set from a single location to illustrate the sensitivity of PSM estimates to variations in PSM methodology and reporting, and (4) provide suggestions for PSM sampling design.

REPORTED PRESPAWN MORTALITY RATES

To illustrate large-scale patterns, we retrieved PSM estimates from peer-reviewed literature and agency reports and compiled data across years and streams. To minimize bias associated with small sample size and male data (discussed below), we only included female PSM rates for sites with more than 20 carcasses recovered per year. Most available PSM estimates were published in annual agency reports and may be preliminary, and PSM estimation methods varied among publications. Given potential methodological biases, we expect the data shown in the PSM summary to reflect relative patterns rather than precise PSM rates.

Reported PSM varied considerably among species and geographic locations (Figure 1; Appendix 1). PSM estimates for late-run Sockeye Salmon in the Fraser River and for Coho Salmon in the Puget Sound region ranged from near 0% to more than 90% in some streams and years. In contrast, PSM was consistently lower than 35% for Puget Sound summer–fall Chinook Salmon. In the mid-Columbia and Snake River regions, spring Chinook Salmon PSM rates were higher and more variable than fall Chinook Salmon rates, although sample sizes for the latter were much smaller. In California's Klamath, Sacramento, and San Joaquin river systems, reported PSM rates were typically less than 30% across species and life history types.

Some of the observed patterns in PSM rates among species may result from differences in life history characteristics and physiology. Spring and summer Chinook Salmon, as well as some Sockeye and Coho salmon, enter freshwater several months prior to spawning (Quinn 2005). These populations are thus susceptible to energetic depletion and environmental stressors such as poor water quality, high water temperatures, and disease expression during their extended holding period. In contrast, many fall Chinook, Chum, and Pink salmon typically enter freshwater shortly before spawning and spend less time in freshwater (Groot and Margolis 1991) but often spawn at higher densities and may be more susceptible to density-dependent processes (Murphy 1985). Observations in Puget Sound streams suggest that Coho Salmon may be more sensitive to toxins in urban runoff than sympatric Chum Salmon (Scholz et al. 2011).

PRESPAWN MORTALITY METHODOLOGY QUESTIONNAIRE

Questionnaire Distribution and Respondents

We distributed an online questionnaire to 81 individuals from 23 organizations that routinely monitored PSM in Pacific salmon throughout the United States and Canada within the past five years. The purpose was to gather information about PSM methodology, potential biases, and common observations. Though we attempted to be comprehensive, the responses to the questionnaire do not represent a complete summary of locations

Table 1. Types of organizations from Alaska, British Columbia, California, Idaho, Oregon, and Washington that responded to the prespawn mortality questionnaire and the numbers and percentages of respondents in each category.

Organization type	AK	BC	CA	ID	OR	WA	%
Consultant	0	0	0	0	0	1	2
Federal	0	5	2	1	0	4	20
Nongovernmental organization	1	0	1	0	0	1	4
Public utility district	0	0	1	0	0	1	4
State	0	0	5	4	4	9	38
Tribal	0	0	0	7	6	4	28
University	1	0	0	0	1	1	4
Total	2	5	9	12	11	21	100

Photo 1. A Coho Salmon prespawn mortality in the Puget Sound area of Washington showing 100% egg retention, with loose eggs inside the body cavity. Photo credit: NOAA Northwest Fisheries Science Center.

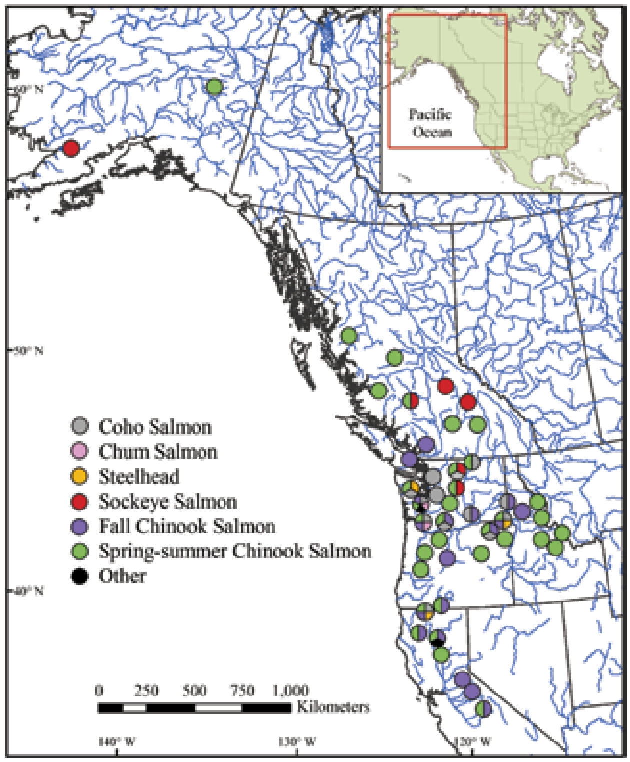

Figure 2. Map of western North America showing locations where questionnaire respondents evaluated prespawn mortality for various salmonid species. Multiple responses were combined where locations overlapped, and locations are approximate due to the map scale. The category "other" depicts sea-run Cutthroat Trout *O. clarkii* in Washington and late-fall/winter Chinook Salmon in California.

where PSM was monitored. The questionnaire had 36 questions, mostly multiple choice, that allowed comparison of responses but necessarily omitted some methodological nuances and location-specific details. Where appropriate, text entry boxes allowed for further explanation. We solicited clarification in follow-up interviews when answers were ambiguous. Multiple responses to individual questions were permitted, so response percentages could exceed 100%.

A total of 60 (74%) individuals from 21 (91%) organizations completed the questionnaire. Respondents included fisheries professionals from state and federal agencies, Native American tribes, public utility districts, nongovernmental organizations, universities, and consulting firms (Table 1). These organizations evaluated PSM in Pacific salmon species in Alaska, British Columbia, California, Idaho, Oregon, and Washington (Figure 2). The respondents had collected PSM data for 1 to 75 years in more than 500 unique streams encompassing nearly 9,000 km of spawning habitat. The focal species or life history type was usually one of local conservation or economic importance. For example, efforts focused on populations listed as threatened under the U.S. Endangered Species Act, such as spring–summer Chinook Salmon in the Snake River and winter-run Chinook Salmon in the Sacramento River, and populations of economic importance, such as Sockeye Salmon in the Fraser River.

Methods Used to Evaluate Prespawn Mortality

Carcass-Based PSM Estimates

Ninety-two percent of respondents used "carcass-based" PSM estimates, in which adult carcasses were collected in holding and spawning areas, and the body cavities were examined. Egg retention in female carcasses was most often estimated visually (78%), although some fisheries professionals counted (17%), weighed (2%), or measured the volume (10%) of eggs.

Annual PSM rates were typically estimated as the ratio of unspawned to total number of carcasses recovered and were usually not weighted by sampling interval. Other fisheries professionals used minor variations in methods to estimate female PSM based on carcass data and reported estimates as egg retention rates or spawning efficiency (e.g., Gilhousen et al. 1990; Fukushima and Smoker 1997; Quinn et al. 2007). Carcass surveys were usually conducted on foot in small streams, by boat in larger rivers, or using a combination of the two. In a few locations, snorkeling was used to recover carcasses from deep pools, or a weir was used to collect carcasses that floated downstream from spawning areas. Carcass surveys were often performed in conjunction with redd count surveys and were also used to estimate abundance, fecundity, size distribution, annual age class composition, sex ratio, and percentage hatchery origin, as well as to collect genetic and pathology samples.

Several factors warrant consideration when estimating carcass-based PSM. The probability of recovering a carcass may vary spatially and temporally due to a number of factors, including stream size, discharge and water clarity, observer effort and experience, and fish behavior (e.g., fish that die while holding in deep pools may have a lower detection probability than fish that die in shallow areas). Carcass recovery probabilities may increase with fish size (Zhou 2002), vary by sex (Murdoch et al. 2010), or be affected by size- or sex-selective predation (Quinn and Kinnison 1999). Additionally, systematic differences among carcass-based PSM estimates may arise from variations in sampling and reporting as described in subsequent sections.

Important differences existed in carcass data collection and reporting that could produce biased PSM estimates: criteria for defining PSM differed among research programs, most respondents only evaluated female carcasses, and PSM calculations differed based on the cause of mortality.

Escapement-Based PSM Estimates

Eight percent of respondents used "escapement-based" PSM estimates, calculated as the inverse of spawner success, using independent estimates of female escapement (potential female spawners) and successful spawners, where Percentage PSM = (1 − Number of redds observed/Estimated female escapement) × 100. Female escapement was estimated at a single location along the migration route, typically a dam or weir, and then adjusted for captured broodstock and harvest upstream from the counting site. When sex was not identified for individual fish, female escapement was estimated using sex ratio. The number of successful female spawners was estimated from redd counts, adjusted by the ratio of redds per female and/or observer efficiency when necessary.

Potential error sources for escapement-based PSM estimates include undercounts or overcounts at counting stations (Boggs et al. 2004), incorrect identification of sex, annual variability in male : female ratios (Murdoch et al. 2010), unreported catch, and redd count errors. Redd count inaccuracies may result from observer error (Dunham et al. 2001; Paulsen et al. 2007), variation in the number of redds per female, low detection rates due to high flows or turbidity (Gallagher and Gallagher 2005), and inaccuracies related to sampling frequency or site selection (Isaak and Thurow 2006). Additionally, if escapement estimates are made downstream along the migration route, escapement-based PSM estimates likely include some en route mortality and, thus, systematically overestimate PSM compared to carcass-based PSM estimates.

Variations in Carcass Data Collection

Important differences existed in carcass data collection and reporting that could produce biased PSM estimates. First, criteria for defining PSM differed among research programs. Questionnaire respondents defined a female PSM as a carcass with 100, 90, 75, 66, 50, 25, or 10% of its expected number of eggs remaining, and others simply reported the estimated percentage spawned for each carcass. Although many respondents indicated that partially spawned carcasses were rare (i.e., females either retained nearly all eggs or <500), a few respondents observed numerous partially spawned carcasses, and changes in the proportion of partially spawned females have been associated with spawner density (Quinn et al. 2007). Thus, differences in the egg retention threshold used during surveys have the potential to influence PSM estimates.

Second, most respondents (61%) only evaluated female carcasses for PSM estimates because of uncertainty associated with differentiating spawned and unspawned males. The

Photo 2. Postmortem summer-run Chinook Salmon found during a carcass survey in the South Fork of the Salmon River, Idaho. Discoloration and wear on the female's tail (background) is indicative of having spawned, as confirmed by examination of the body cavity. Photo credit: Tracy Bowerman.

Photo 3. Postmortem female summer-run Chinook Salmon carcass with a worn tail, indicative of having spawned, South Fork Salmon River, Idaho. Photo credit: Tracy Bowerman.

Photo 4. Spring Chinook Salmon prespawn mortality with intact egg skeins and no wear on the tail. Recovered in the Willamette River Basin, Oregon. Photo credit: Grant Brink/George Naughton, University of Idaho.

remainder of respondents either used carcasses recovered prior to spawning initiation to estimate male PSM (26%) or visually inspected male carcasses during the active spawning period and considered those with thin, flaccid testes fully spawned and carcasses with full, firm testes unspawned (13%). Inclusion of males can substantially influence PSM estimates because of potential sex-specific differences in the probability of carcass recovery and mortality.

Third, PSM calculations differed based on the cause of mortality. Most respondents (82%) included all mortalities in their PSM estimates, regardless of cause of death, and the remaining respondents (18%) excluded carcasses if they showed signs of predation or fishing-related injury. Either approach may be appropriate depending on monitoring goals, but excluding some mortality sources will underestimate total PSM.

Temporal and Spatial Variations in Carcass Sampling

The timing of carcass surveys relative to the spawning season differed among programs. Fifty percent of respondents regularly surveyed streams prior to the initiation of spawning ("pre-redd PSM").Others restricted surveys to the spawning season ("spawning period PSM"), beginning surveys once spawning activity was observed (33%) or surveying only during the peak of spawning (7%). A few respondents only included carcasses recovered prior to the onset of spawning (2%) and for the remainder, timing varied annually depending upon budgets and staffing (8%). Several respondents did not regularly conduct carcass surveys prior to spawning but did observe periodic fish die-offs during that time. Notably, mortalities in early die-off events were not always included in PSM estimates.

The frequency of carcass surveys varied among respondents. Populations were surveyed daily (6% of respondents), two or more times per week (20%), weekly (57%), every other week (9%), annually (4%; found in a few remote study areas), and, in some locations, survey frequency varied among sites and years (4%). Many questionnaire respondents reported that frequent sampling and high effort were needed to recover a sufficient number of carcasses for reliable PSM estimates due to small population sizes or because carcasses quickly decomposed or were scavenged.

The spatial extent of spawning areas surveyed for carcasses varied among locations. Most respondents (68%) conducted a complete census of the spawning area, whereas others restricted surveys to index reaches (14%), areas with high-density spawning (11%), or accessible locations (7%). In addition to regular carcass surveys, some respondents conducted random surveys outside of known spawning areas (7%) or opportunistic surveys where mortalities were known to occur (11%). Respondents also noted substantial spatial variability in PSM estimates in relation to spawner density and differences in carcass recovery probabilities due to habitat, water quality, and stream size.

SENSITIVITY OF PSM ESTIMATES TO METHODOLOGY

Sensitivity to Variations in Carcass Data

We used a detailed data set of escapement and carcass recovery data from a summer-run Chinook Salmon population in central Idaho to illustrate how variations in methodology and reporting can affect PSM estimates. Carcasses were recovered during repeated censuses of the South Fork Salmon River spawning area. Carcass surveys were conducted weekly, beginning four or five weeks prior to spawning and ending approximately one week after the last redd was observed. Based on visual estimates of the percentage of eggs retained, female carcasses were classified as unspawned (>75% retained), partially spawned (25–75% retained), or successful (<25% retained). Annual female PSM was estimated as the number of unspawned female carcasses divided by the total number of female carcasses collected. Only males found dead prior to observed spawning were used to estimate male PSM. Hence, male PSM was estimated as the number of male pre-redd carcasses divided by the total number of males recovered that year. These data were chosen because of their high spatial and temporal resolution, but two factors potentially influenced PSM estimates in this population. First, fish were captured and passed upstream of a weir that marked the bottom of the study area, and associated handling may have increased mortality. Second, a large number of carcasses were recovered washed up against the weir, which increased carcass recovery probability, particularly prior to spawning.

In the first sensitivity analysis, we estimated PSM using seven subsets of carcass data from two years (2003 and 2009) with different sample sizes. Each data subset, or scenario, represented a methodological variation in how carcass data could be collected and compiled (Table 2). Scenario A estimated PSM using all unspawned females recovered in the primary spawning area. This scenario was commonly reported in questionnaire responses, and we considered it the reference estimate. Scenario B examined the effect of egg retention cutoffs on PSM estimates by including partially spawned females. Scenario C examined the effect of changing the sampling schedule by halving the sampling frequency while sampling at regular intervals throughout the survey period. Scenario D examined the effect of including males in PSM estimates. Scenario E examined the effect of variations in carcass recovery probability and spatial sampling area by excluding carcasses recovered from the weir and the stream section directly upstream of the weir. The last two scenarios examined the effect of survey timing relative to the onset of spawning by using a subset of data in which surveys began approximately two weeks prior to spawning onset, rather than four (2003) or five (2009) weeks prior in Scenario F, and including only surveys conducted during the spawning period in Scenario G.

Baseline estimates of PSM (Scenario A) were 56% in 2003 and 43% in 2009 (Figure 3). Inclusion of partially spawned females (Scenario B) resulted in PSM estimates that were very similar to Scenario A. With halved effort distributed evenly throughout the sampling period (Scenario C), the PSM estimate in 2003 was 3% higher than the Scenario A estimate and the 2009 estimate was 3% lower. These differences would be exacerbated if PSM was episodic within season, as has been observed in other systems (Fukushima and Smoker 1997; Quinn et al. 2007). When male data were included (Scenario D), the PSM estimate in 2003 was 14% lower than in Scenario A and the 2009 estimate was 19% lower. PSM estimates were substantially lower for males than females, largely because only male mortalities found prior to the spawning season were used in estimates. Omission of carcasses recovered at the weir and the lowermost end of the spawning area (Scenario E) substantially reduced the total number of recovered carcasses (Table 2) and resulted in PSM estimates that were 51% (2003) and 34% (2009) lower than those in Scenario A. When carcass surveys began two weeks prior to spawning (Scenario F), PSM estimates were 25% (2003) and 14% (2009) lower than Scenario A estimates because considerable PSM occurred early in the holding period. Carcass surveys conducted only during the spawning season (Scenario G) resulted in PSM estimates that were 53% (2003) and 35% (2009) lower than Scenario A estimates, demonstrating that surveys conducted only during active spawning dramatically underestimated total PSM for this population.

The escapement-based approach may be prone to overestimating PSM because uncounted redds are attributed to PSM, including those outside survey areas. On the other hand, carcass-based PSM estimates may tend to underestimate PSM due to low carcass recovery probabilities and lack of sufficient data prior to the spawning season.

Carcass-Based versus Escapement-Based PSM

In a second set of comparisons, we evaluated differences between carcass-based (Scenario A above) and escapement-based PSM estimates in the South Fork Salmon River from 2002 through 2007. For escapement-based estimates, annual escapement was the number of females passed above the weir, and sex was determined from morphological characteristics. Most fish passed the weir between June 25 and August 1, and spawning typically occurred between August 13 and September 13. Spawner abundance was estimated from redd counts, conducted weekly, assuming a complete census of spawning habitat and a 1:1 female spawner-to-redd ratio (a common assumption for Chinook Salmon; Gallagher and Gallagher 2005; Murdoch et al. 2009). Observer efficiency during redd counts was assumed to be 100% (i.e., all redds upstream of the weir were counted).

Carcass-based PSM estimates were considerably lower than escapement-based PSM estimates in all years except 2003 (Figure 4). Carcass-based PSM estimates ranged from 11% to 57% (mean = 32%), whereas escapement-based estimates ranged from 47% to 83% (mean = 71%). Escapement-based PSM estimates that were repeatedly higher than carcass-based estimates have been reported in other locations where both approaches were used simultaneously (Schroeder et al. 2005; Snow et al. 2011).

Consistent discrepancies between escapement-based and carcass-based PSM estimates here and in other systems highlight

Box 1. Recommendations for monitoring PSM in salmon populations using carcass survey data.

The following data collection considerations can help maximize sampling efficiency, improve accuracy of PSM estimates, and facilitate comparisons among populations and across sites and years. Sample size and PSM calculation methods should be explicitly stated. Carcass detection probabilities and sample size necessary for a given level of precision should also be considered (see text for details). For more information on developing aquatic monitoring designs, visit monitoringadvisor.org, and for examples of carcass count and redd survey protocols, see stateofthesalmon.org/fieldprotocols and fishandgame.idaho.gov/ifwis/portal/sites/ifwis/files/fisheries/SGS/SGS_ManualStandardProcCountingChinookRedds.pdf.

- **Spatial design:** Because variation in PSM rates can occur within a single stream, monitoring programs should strive to have a spatially balanced design. Censuses of entire spawning areas will provide the most complete estimate, but spatially balanced random samples may suffice.
- **Temporal design:** Considerable variation in PSM rates can occur prior to spawning initiation and throughout the spawning season. Surveys that begin shortly after fish arrive in holding/spawning areas and continue to the end of spawning will be most representative of annual PSM rates.
- **Sampling frequency:** Frequent surveys (e.g., weekly) evenly distributed throughout the holding and spawning period can be robust to temporal variations in mortality and allow for better inference about timing and cause of death. Effective survey intervals will depend on river conditions, rate of decomposition, carcass scavenging rates, and spawner density.
- **Sex differentiation:** Most studies only include PSM data on females; if males are evaluated for PSM, rates for the two sexes should be reported separately.
- **Criteria for determining PSM:** The following cutoffs for female carcasses are common and useful for visual estimates: >75% egg retention = unspawned, 25%–75% egg retention = partially spawned, and <25% egg retention = fully spawned. Partially spawned and unspawned observations should be summarized separately to facilitate consistent comparisons.
- **Cause of death:** If a distinction is made regarding the cause of death (e.g., unexplained vs. predator-related mortality), estimates should be reported separately to improve resolution on causation and to provide comparable estimates across studies.

Table 2. Description of the scenarios used to illustrate differences in annual prespawn mortality rates based on different subsets of a single carcass survey data set, collected in central Idaho on a population of Snake River summer-run Chinook Salmon. Unless otherwise specified, data represent female carcasses collected during eight complete censuses of the spawning area, conducted approximately weekly, beginning four (2003) and five (2009) weeks prior to the initiation of spawning and ending after spawning had ceased. Sample sizes of PSM and presumed successfully spawned (S) carcasses are shown.

Scenario	Description of data used	2003		2009	
		PSM	S	PSM	S
A	Percentage of carcasses that retained >75% eggs	378	292	51	68
B	Percentage of carcasses that retained >25% eggs	380	290	52	67
C	Subsample of dates randomly chosen to represent surveys conducted approximately every four weeks	255	178	35	53
D	Male and female carcasses included in PSM estimate; only male carcasses recovered prior to spawning were included	591	805	63	196
E	Spatial data subset: carcasses recovered at weir and river section directly upstream of weir were excluded	12	212	4	42
F	Carcass surveys began two weeks prior to spawning	136	292	27	68
G	Carcass surveys were conducted only during spawning period	11	285	6	68

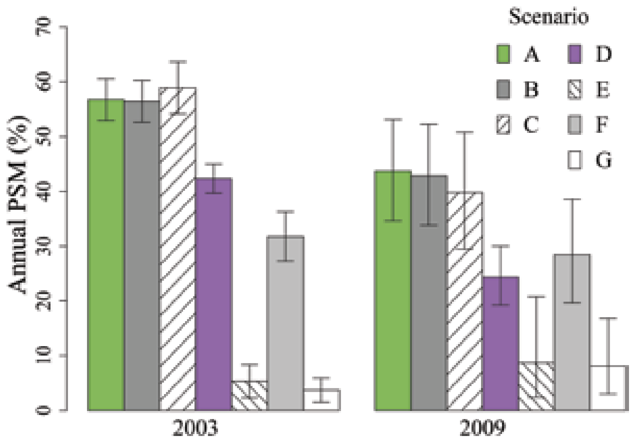

Figure 3. Annual percentage PSM estimates using seven different subsets of a single spring–summer Chinook Salmon carcass-based data set, collected in central Idaho, 2003 and 2009. Error bars show 95% confidence intervals. Scenarios are described in the text and in Table 2.

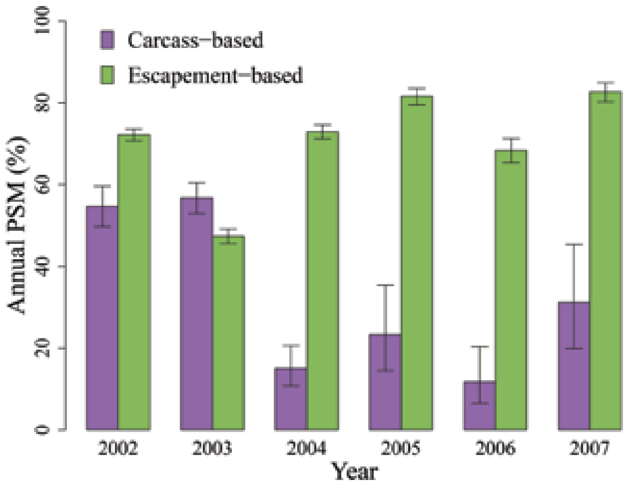

Figure 4. Annual percentage female PSM from carcass-based estimates (PSM = [Number of unspawned female carcasses/Total carcasses recovered] × 100; purple bars) and escapement-based estimates (PSM = [1 − Number of redds observed/Number of redds expected given the number of females passed above a barrier weir] × 100; green bars). All data are from a single population of spring–summer Chinook Salmon in central Idaho. Error bars show 95% confidence intervals.

the need for further research to determine the primary sources of bias in each method, which could vary among locations and species. The escapement-based approach may be prone to overestimating PSM because uncounted redds are attributed to PSM, including those outside survey areas. On the other hand, carcass-based PSM estimates may tend to underestimate PSM due to low carcass recovery probabilities and lack of sufficient data prior to the spawning season. Importantly, carcass-based approaches allow for determination of whether individuals successfully released gametes and may provide additional information on proximate mortality causes (e.g., predation, disease, etc.). A more complete understanding of the types and magnitude of estimation biases and errors associated with each of these approaches could be achieved through intensive PSM monitoring and targeted investigation into the sources of bias and error. Such research would likely yield other important information regarding the timing, location, and causes of mortality.

STUDY DESIGN CONSIDERATIONS

Based on questionnaire responses and information from published reports, we identified several important study design and reporting considerations that could help improve the accuracy and precision of carcass-based PSM estimates (Box 1). A single sampling protocol or set of recommendations is not practical for all research programs, but efforts to standardize data collection and reporting and improve sampling designs would be broadly beneficial. To provide consistent PSM estimates among years and locations, the following categories should be reported separately: males and females, unspawned and partially spawned carcasses, and cause of death if such a distinction is made. Within the monetary and logistical constraints of each research program, study designs should strive to be balanced spatially and temporally, have an adequate sample size, and consider carcass recovery probability.

Carcass surveys should begin as soon as fish arrive in spawning streams because mortality during the holding period prior to spawning can be substantial and strongly influence PSM estimates, as in our case study. Surveys conducted only during the spawning season may dramatically underestimate total PSM, especially for populations with an extended holding period. Additionally, PSM rates may vary considerably throughout the

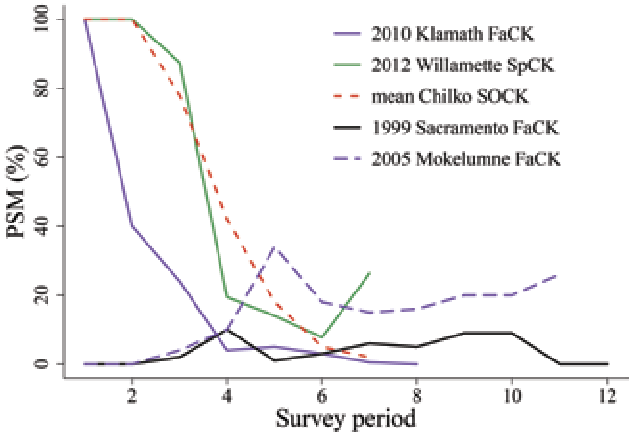

Figure 5. Within-year PSM estimates by survey period for populations of fall Chinook (FaCK), spring Chinook (SpCK), and Sockeye (SOCK) salmon. Data from Gough and Williamson (2013; Klamath River, CA), University of Idaho (unpublished; North Fork of the Middle Fork Willamette River, OR), Gilhousen et al. (1990; Chilko River, BC), Snider et al. (2000; upper Sacramento River, CA), and Workman (2006; lower Mokelumne River, CA).

Photo 5. Carcass of a fully spawned spring Chinook Salmon with only a few eggs remaining in the body cavity. Photo credit: Grant Brink/George Naughton, University of Idaho.

sampling period. A pattern of decreasing PSM rates throughout the survey period has been documented for spring-run and fall-run Chinook Salmon, as well as Sockeye Salmon populations (Figure 5). Therefore, carcass surveys should be conducted frequently to provide estimates that are representative of overall seasonal averages. If frequent surveys are not possible, surveys should be temporally distributed throughout both the holding and spawning periods, and development of an area under the curve approach may be appropriate (Hilborn et al. 1999). In contrast, some fall Chinook Salmon populations showed relatively consistent PSM rates over time (Figure 5), probably because fish arrived at spawning areas shortly before spawning and thus were exposed to potential stressors over a shorter time period. In populations that exhibit consistent PSM rates throughout the season, less frequent monitoring may suffice.

Monitoring programs should strive to have a spatially balanced design because factors associated with both PSM and carcass recovery probability can vary spatially within a single stream system (e.g., fish density and water clarity). Repeated censuses of spawning and holding areas often provide a more accurate measure of PSM, but this strategy may be infeasible in some locations and may not be the most efficient allocation of available resources for large study areas. Index reaches are commonly used and can provide valuable time series information, but data from non-randomly selected index areas may not be representative of the population and may miss important annual and spatial variations (Isaak and Thurow 2006; Courbois et al. 2008). Spatial sampling designs, such as systematic sampling, stratified random sampling, or a spatially balanced randomized design, will typically provide a more representative subsample (Courbois et al. 2008; Larsen et al. 2008). Sample unit size and sampling proportion will depend upon the size of the population and the study area.

Biases in carcass detection probability should also be considered. Biases may vary considerably among sites, and research to evaluate carcass detection probabilities (e.g., by mark–recapture of carcasses; Bare et al. 2014) will help surveyors understand the magnitude and source of such biases. If an estimate of carcass observer efficiency is established, an expansion factor could be applied to estimate the total number of carcasses missed.

After carcass detection biases have been addressed, a sufficient sample size of recovered carcasses is still required to achieve precise estimates of PSM. The necessary sample size for a proportion (assuming a binomial distribution) will depend upon the population size, expected proportion, and the desired margin of error and confidence level (Krebs 1999). Estimating variance associated with a specific spatial or temporal sampling design requires additional sample size considerations (Courbois et al. 2008). Reported PSM rates should include information on sample size and some indication of effort to allow readers to judge the reliability of estimates. Obtaining reliable PSM estimates for very small populations will likely remain a challenge because of small sample sizes and low detection probability.

Escapement-based PSM estimates could be improved by reducing errors in both escapement and redd counts and, where appropriate, adjusting these numbers based on estimates of passage efficiency at escapement locations, the number of redds per female, and redd observer efficiency (e.g., Gallagher and Gallagher 2005). Other potential sources of bias should also be evaluated, such as en route mortality that occurs above the escapement estimate location and spawning that occurs outside the redd survey area.

SUMMARY

PSM is a widespread phenomenon in many Pacific salmon species as well as in iteroparous salmonids (DeRito 2004). The high level of PSM observed in some Pacific salmon populations could have profound effects on overall production and could be a serious impediment to recovery of declining stocks. As such, reliable PSM estimates are important for implementation of fisheries quotas and to evaluate the long-term viability of at-risk populations. Currently, detailed reporting of PSM rates and information about methodology is scarce in the primary literature, despite prevalent PSM monitoring throughout the Pacific region. PSM estimates may be subject to considerable measurement error and potential biases.

However, accuracy and repeatability can be improved through study design modifications and future research to evaluate factors contributing to errors and biases. Research evaluating the relative performance of different methods used to estimate PSM will provide more prescriptive sampling recommendations and improve inferences from PSM monitoring that help guide management actions.

Although proximate causes of PSM may vary among locations and species, multistock comparisons can help fisheries professionals better understand their own study systems and identify factors that may otherwise be overlooked. Ultimately, PSM-related data will be more valuable if it is collected consistently through time, in a way that allows comparisons among populations, and can be scaled up to evaluate regional patterns. Understanding temporal and spatial processes that influence PSM will become increasingly important to ensure sustainable fisheries and effective management of populations that are stressed by ongoing impacts to freshwater habitats (Lackey 2003) and predicted climate-related changes to stream temperatures and flow regimes (Mote et al. 2003; Isaak and Rieman 2013).

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APPENDIX 1. PUBLICATIONS WITH DATA ON PRESPAWN MORTALITY USED TO CREATE FIGURES 1 AND 5

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